SHIFT OF ACTIVITY FROM SLOW TO FAST MUSCLE DURING VOLUNTARY LENGTHENING CONTRACTIONS OF THE TRICEPS SURAE MUSCLES IN HUMANS

BY ANTONIO NARDONE AND MARCO SCHIEPPATI*

From the Istituto di Fisiologia Umana II, Università degli Studi di Milano, Via Mangiagalli 32, I-20133 Milano, Italy

SUMMARY

1. Raw or rectified and integrated electromyograms (integrated EMGs) of the leg muscles were recorded during (a) isotonic ramp shortening or lengthening contractions consisting of foot plantar flexions against a constant load, or dorsal flexions accomplished by braking the load and yielding to it, respectively, and (b) isometric increasing or decreasing plantar torques accomplished by graded contractions or relaxations of the triceps muscles.

2. During plantar flexions or increasing torques, the EMG of soleus, gastrocnemius lateralis, medialis, and peroneus increased in parallel. During decreasing torques, motor unit derecruitment took place gradually and simultaneously. The tibialis anterior was silent. During dorsal flexions, one of two characteristic patterns was observed in different subjects: (a) soleus was abruptly derecruited at the beginning of the task, while gastrocnemius lateralis (or medialis) exhibited a large recruitment lasting throughout the lengthening contraction; (b) soleus remained active during the task, showing large motor unit potentials, while the gastrocnemius lateralis recruitment was of a lesser extent than in (a). Peroneus derecruitment was gradual and tibialis anterior activity was absent in both cases.

3. The EMG patterns observed during plantar flexions or in increasing and decreasing torques, and the two patterns observed during shortening or lengthening contractions, were closely reproduced during sinusoidal oscillations of the foot or in isometric contractions and relaxations.

4. When recruitment of the gastrocnemius lateralis was present during dorsal flexion, the slope of its integrated EMG envelope was steeper, the higher the velocity of lengthening contraction. The most rapid and the slowest tasks, however, did not require its activation. Gastrocnemius lateralis integrated EMGs of an amplitude similar to those occurring during lengthening contractions were observed only during ballistic plantar flexions.

5. The two patterns of triceps activation occurring during lengthening contraction could be traced to different mechanical characteristics of the soleus muscles, the gastrocnemius lateralis being activated preferentially in subjects with long soleus

* To whom all correspondence should be addressed.

half-relaxation times, and the soleus in subjects with short soleus half-relaxation times.

6. The soleus and gastrocnemius lateralis H reflexes were tested during shortening and lengthening contractions. Under these conditions, their amplitudes increased above rest values during shortening contractions; during lengthening contractions, both reflexes decreased to well below rest values regardless of the pattern of activation of the corresponding muscles during dorsal flexion.

7. The results indicate that voluntary triceps surae lengthening contractions are performed by derecruitment of slow muscles or motor units, accompanied by selective activation of fast muscles or motor units. The mechanical advantage of this behaviour is considered, and the possible neural mechanisms responsible for it are discussed, including presynaptic and recurrent inhibition.

INTRODUCTION

Many investigations have dealt with the question of motoneurone recruitment in both animals and man (see Burke, 1981; Clamann, 1981; Edström & Grimby, 1986, for recent reviews). It is safe to say that the orderly recruitment of motor units according to the 'size' principle (Hennemann & Mendell, 1981) is a general rule which governs force coding. This implies that slow-contracting motor units, innervated by small and slowly conducting motoneurones, fire before rapidly contracting ones both in ramp and ballistic isometric contractions (Desmedt, 1983).

Deviations from this recruitment order appear to be rather infrequent: they have been shown under conditions in which the motoneurone pool is the target of peripheral inputs (in the cat: Creed, Denny-Brown, Eccles, Liddell & Sherrington, 1932; Kanda, Burke & Walmsley, 1977; Dum & Kennedy, 1980; in man: Garnett & Stephens, 1981), of labyrinthine (Denny-Brown, 1929) or rubrospinal inputs in the cat (Hongo, Jankowska & Lundberg, 1969; Burke, Jankowska & ten Bruggencate, 1970), or during very fast automatic movements, such as bicycling at high rates in man (Citterio & Agostoni, 1984) or paw shaking in cats (Smith, Betts, Edgerton & Zernicke, 1980), during which the fast-twitch motor units are activated while slow-twitch ones may be silenced.

Motoneurone rank ordering makes sense from a metabolic (Burke, 1981) and a behavioural (Hennemann & Mendell, 1981) point of view, except possibly during the most rapid movements. Even in this case, however, the unloading of active slow-twitch units would lead to a waste of energy to only a limited extent, since the heat generated by a muscle increases proportionately with the load against which it contracts (Hill, 1964). Thus, the only factor changing as a function of the speed of contraction is the force level at which the motor units are recruited. In man, during fast-ramp or ballistic contractions, the motor units fire earlier (at a lower force level) than during slow-ramp contractions, although in the usual rank order, and this assures a timely force contribution to the force output of the whole muscle (Büdingen & Freund, 1976). Changing the task from isometric to isotonic does not seem to alter the order of recruitment (Grimby, 1984).

If the motor units' contraction times are relevant to the speed of force development during isometric or shortening contractions, however, one can easily foresee that

equal importance should be given to relaxation times under the conditions of isometric relaxations or lengthening contractions. Both conditions underlie common modes of motor behaviour: the latter is exemplified by a subject holding a weight in his hand with the forearm flexed and dropping it carefully by controlled relaxation of the biceps muscle, or, in the case of the triceps surae, when one descends stairs. This implies muscle contraction while lengthening, in the period between contact of toe tips and heels, in order to brake the body's fall.

The question therefore arises of how the tasks involving lengthening of active muscle can be properly executed if the intended velocity of lengthening must exceed that imposed by the motor units' relaxation time. Even assuming that the whole muscle would be silenced, the consequent muscle lengthening could not exceed (taking into consideration the weight of the load opposing the contraction) a given velocity imposed by the relaxation times of the slowest motor units. In fact, the latter should have been the active ones at the beginning of the task, as predicted by the size principle. The difficulties inherent in this motor behaviour could certainly be overcome by contraction of the muscle(s) antagonist to those undergoing a lengthening contraction, but co-contraction, in addition to being more costly from a metabolic point of view, would put a greater burden on the central nervous system in terms of neural control.

It may be hypothesized that for correct performance of a voluntary lengthening contraction, such as yielding to a load at controlled velocity, the derecruitment of fast contracting–fast relaxing motor units of the agonist muscle would be more advantageous than the derecruitment of slow motor units, since the force developed would terminate earlier in the former than in the latter, placing more 'handy' quanta of force at the disposal of the central nervous system. Since, during shortening or tonically maintained contractions, the slow motor units sustain the force, this necessarily implies as a corollary that at some time prior to or during the task, the slow units are derecruited and the load is taken over by fast ones.

In this paper, the question will be dealt with by studying the surface electromyographic activity of the soleus and the gastrocnemii muscles during shortening and lengthening contractions. The different motor unit composition of the soleus muscle with respect to that of the gastrocnemii – the slow-twitch motor units being rather segregated in the soleus – gives the opportunity of getting information about the relative involvement in the two tasks of motor pools having different characteristics, simply by means of surface recording. In addition, the easy access to their motor nerves allows us to investigate their reflex excitabilities under the two conditions by means of the H reflex (see Schieppati, 1987). In a previous paper from this laboratory, in fact, evidence was given to show that changes in reflex excitability of the soleus motor pool, probably of presynaptic origin, may serve the purpose of modulating motoneurone recruitment during voluntary shortening and lengthening contractions in order to match muscle mechanical characteristics with intended behaviour (Romanò & Schieppati, 1987).

METHODS

Eleven volunteers (three females and eight males) between 16 and 39 years of age participated in this study. They sat in an examination chair with the knee and ankle joint angles at 110 and 85

deg of rotation, respectively (rest position). The right foot was strapped to a mould mounted on a metal plate, allowing a plantar rotation of 25 deg about an axis through the medial malleolus. The foot position was recorded by a liner potentiometer centred on the axis of rotation. One end of a flexible steel wire was attached to the plate at a point corresponding to the position of the metatarso-phalangeal joints. The other end of the wire carried a load which exerted a force of 100 N upon the foot plate so that the load opposed plantar flexion of the foot. A block prevented the load from passively dorsiflexing the foot beyond the rest position, since the load was sufficient to pull the unrestrained foot up to about 70 deg, at which angle the triceps length was such that its elastic elements took over the weight. The wire ran over two ball-bearing pulleys held in position by a metal frame in such a way that the direction of force was approximately parallel to the long axis of the soleus muscle, and this parallelism was preserved throughout the 25 deg rotation of the tibio-tarsal joint. As a result of this arrangement, the force at the plate remained constant irrespective of the foot rotation (Romanò & Schieppati, 1987). Alternatively, the plate was fixed to a strain gauge in order to measure the torque exerted by plantar efforts.

An oscilloscope was mounted on the frame in front of the subject; the screen displayed the angular rotation of the foot, or the torque, as a vertical deflection of a spot, while the time base could be set in free-run mode at different velocities. The subjects were instructed to keep the spot within a narrow double track patterned on the screen, featuring a linear change in foot position (isotonic condition) or torque (isometric condition) at various rates, in both plantar and dorsal direction. The plantar flexion was achieved by a controlled shortening contraction of the triceps muscles starting from rest position, while the dorsal flexion was initiated from an actively maintained plantar flexion (holding the 100 N load in position) of a few seconds durations, and was brought about by the subject allowing the load to dorsiflex the foot gradually, by simply opposing its dorsiflexing action with a graded triceps lengthening contraction and yielding to it until foot rotation eventually reached rest position. Likewise, the isometric task consisted of increasing or decreasing the torque by controlled contraction or relaxation, respectively, of the triceps surae muscles. The maximum torque was usually equal to that reached during the holding phase of the isotonic task. Both the torque level and the tibio-tarsal angle (foot in rest position, plantarflexed, or in mid-position) had no relation with the EMG patterns observed during muscle activation and relaxation. All the tasks were achieved with little practice regardless of beam velocity (rate of change in force or position) or direction of angular rotation.

Pre-gelled recording surface electrodes, spaced 1 cm apart, were taped to the rubbed skin on the lower third of the leg posteriorly (soleus), and on the upper third posteromedially (gastrocnemius medialis), posterolaterally (gastrocnemius lateralis), laterally (peroneus), and anteriorly (tibialis anterior). The EMG signals were amplified, bandpass filtered (10–1250 Hz) and/or rectified and integrated (integrated EMG, time constant 10 ms, when not otherwise stated). The computer (Olivetti M24, DT2801 A/D board) performed back-averages of integrated EMGs and movement (or force) of twenty to thirty repetitions of the tasks, triggered by the output of a level discriminator receiving the position (or force) signal. The averaged integrated EMG envelopes were used in an attempt to quantify differences in the muscles' activation patterns within both muscles and subjects during the dorsal flexion task. The integrated EMGs exerted by each triceps muscle during both tonic contraction and dorsal flexion varied in amplitude among subjects, and within subjects according to the velocity of foot rotation. Therefore, to allow comparisons, an index was developed independent of the magnitude of the EMG exerted under tonic condition. This corresponded to the ratio between the amplitude of the averaged integrated EMG recorded midway during flexion and that recorded during the tonic phase (dynamic to tonic ratio, DTR). For example, if the integrated EMG of a given muscle decreased linearly and gradually from the holding position to reach zero at the end of the dorsal flexions, the index corresponded to 0·5. Indexes larger than 1 would point instead to an increased motor unit recruitment (or to a recruitment of larger motor units) during the dorsal flexion rather than in the tonic phase. Since the raw EMG was dominated under the condition of dorsal flexion by high-amplitude potentials, not necessarily superimposed on a background full-interference pattern, a large index value may actually indicate recruitment of fast motor units. This seems likely since (1) the integrated EMG increased in amplitude in spite of steady, or even decreasing, force developed by the muscle (see Citterio & Agostoni, 1984), and (2) fewer motor units must be active, and at lower frequencies of discharge, during lengthening contraction (Joyce, Rack & Westbury, 1969; Romanò & Schieppati, 1987), owing to the larger unitary force developed under this condition (Katz, 1939). Thus, this

index was used to compare the behaviour of the same muscle under different conditions, or to give an indication as to the preferred mode of activation of one muscle over the other in different subjects.

In order to elicit H reflexes in the soleus or the gastrocnemius laterialis muscles, the posterior tibial nerve was stimulated electrically at the popliteal fossa with single pulses of 1 ms duration delivered through a constant-current isolation unit. The cathode was housed in a plastic foam support, held in place against the nerve by means of a rubber band strapped around the leg. The anode was a large silver plate placed on the knee. Stimulus strength was adjusted so that, under control conditions (rest position), the H reflex in either muscle was about half the amplitude of the maximum value it could attain. Electrode position was chosen in such a way that the stimulus evoked a small direct M response. Since half-maximal H reflexes could not be obtained simultaneously from both muscles, the experiments were done consecutively on the same subject during the same session. Stimuli were delivered at rest or during plantar and dorsal flexions at various foot positions under pseudo-random conditions.

The mechanical characteristics of the subjects' soleus muscle were investigated by inducing a twitch through electric stimulation of the inferior soleus nerve (1 ms duration, cathode about 6 cm below insertion of gastrocnemius lateralis into the Achilles tendon, plate anode on the shin) which gave a direct M response in the muscle. This method was preferred to that of stimulating the posterior tibial nerve, or that of directly stimulating the muscle by large plate electrodes, since it avoided activation of the other leg muscles, as monitored by EMG recordings of the gastrocnemius lateralis, medialis, peroneus and tibialis anterior. The appearance of an H reflex upon slight voluntary innervation of the muscle was considered proof that the stimulating electrodes activated the nerve rather than the muscle (Fig. 6*A*). Stimulus strength was adjusted so as to induce twitches of the same peak amplitude in all the subjects, while each was fully relaxed, and with his or her foot in the rest position.

<div align="center">RESULTS</div>

EMG during isometric augmenting or decreasing plantar torques

In all the subjects the soleus, gastrocnemius lateralis, medialis, and peroneus muscles increased or decreased their activity during augmenting or decreasing efforts, respectively (Fig. 1*A* and *B*). In both cases the increase and decrease of the EMG activity showed a roughly parallel time course in all the muscles. During increasing plantar torque, the soleus was activated first and reached a level of activity higher than that in the gastrocnemius lateralis, medialis, or peroneus muscles. During decreasing torque, all the muscles underwent a gradual progressive derecruitment of their motor units. In both tasks the tibialis anterior muscle was silent.

EMG during plantar or dorsal flexions

The pattern of activation of the muscles during plantar flexion was similar to that observed during increasing isometric plantar torques, as shown in Fig. 1*C*. Again, motor unit recruitment was gradual and progressive in all the muscles and in all the subjects. During dorsal flexions, however, starting from a stationary plantar flexion and yielding to the load by controlled muscle relaxation (*D*), the expected gradual derecruitment was observable only in the peroneus muscle. The other muscles' behaviour was at variance with isometric conditions, and, in addition, exhibited a different pattern of activation in the various subjects, ranging between two extremes represented in Fig. 1*D* and *E*. In *D*, the activity in the soleus muscle decreases abruptly to a very low level just prior to the beginning of dorsal flexion, and further decreases during the completion of the task, while that in the gastrocnemius lateralis

increases strikingly above the low level observed during the maintenance phase of tonic contraction, remains high throughout flexion, and ceases at the end of it. In this period the gastrocnemius lateralis EMG displays motor unit potentials of very high amplitude which are not present either under isometric conditions or during plantar flexion. Instead the medial gastrocnemius and the peroneus undergo a gradual
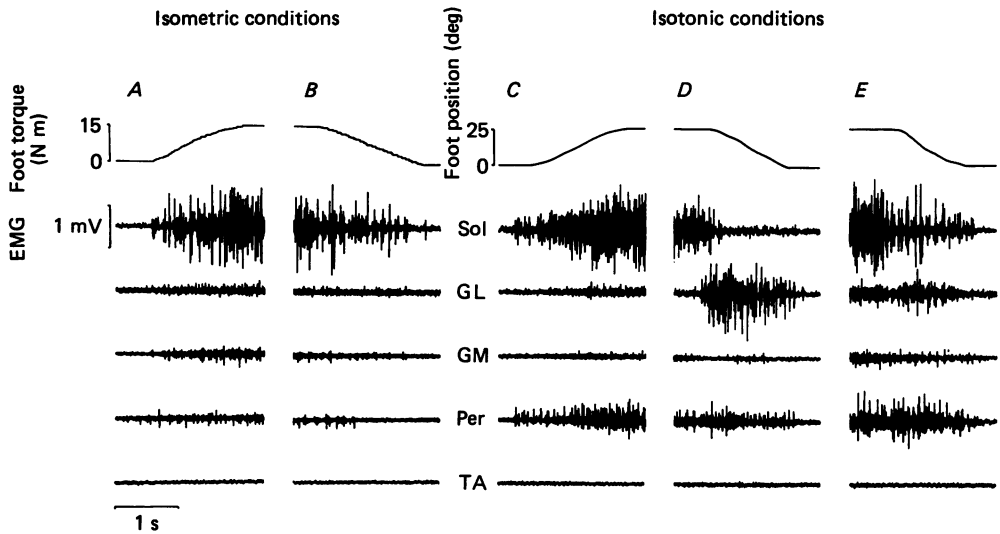

Fig. 1. Patterns of EMG activity of leg muscles during increase (A) or decrease (B) in foot torque, and isotonic plantar (C) and dorsal (D and E) flexions. Isometric conditions: from top to bottom, torque, raw EMG of soleus (Sol), gastrocnemius lateralis (GL), medialis (GM), peroneus (Per) and tibialis anterior (TA) are displayed. During both tasks a gradual increase (A) or decrease (B) of EMGs in triceps and peroneus muscles accompanied force rise or decay, respectively; tibialis anterior was silent. Isotonic conditions: changes in foot position during voluntary plantar flexion against a load of 100 N (C) and during dorsal flexions (D and E, two subjects), performed at an angular velocity of 25 deg/s (top traces). In C, activity of triceps surae and peroneus muscles gradually increases as in A. At variance with B, dorsal flexion (D) is preceded by abrupt decrease of soleus EMG and striking increase of gastrocnemius lateralis EMG, showing large motor unit potentials lasting throughout the task. In E, soleus EMG full-interference pattern decreases prior to dorsal flexion and is substituted by large motor unit potentials superimposed on low-level background activity. In this and in the following Figures, 0 deg corresponds to 85, and 25 to 110 deg of tibio-tarsal joint angle.

derecruitment. In E, the full-interference pattern of soleus EMG also decreased in the period preceding the beginning of the dorsal flexion and was substituted during the dorsal flexion by large bursts of motor unit activity superimposed on a low-level background activity. Little activation was present during dorsal flexion in the gastrocnemii muscles. In this case also, the peroneus muscle showed a gradual derecruitment, and tibialis anterior was silent.

Sinusoidal contractions under isometric or isotonic conditions

The features of the activation pattern under isometric and isotonic conditions were also reproduced in the cases in which isometric contractions and relaxations, or

plantar and dorsal flexions, were performed consecutively, so as to produce a series of sinusoidal changes in force or angular foot positions. The left panel of Fig. 2 shows two cycles of sinusoidal isometric contractions which display gradual EMG recruitment and derecruitment during force rise and decay, respectively, whose pattern and time course is comparable in all the muscles. The right panel shows that
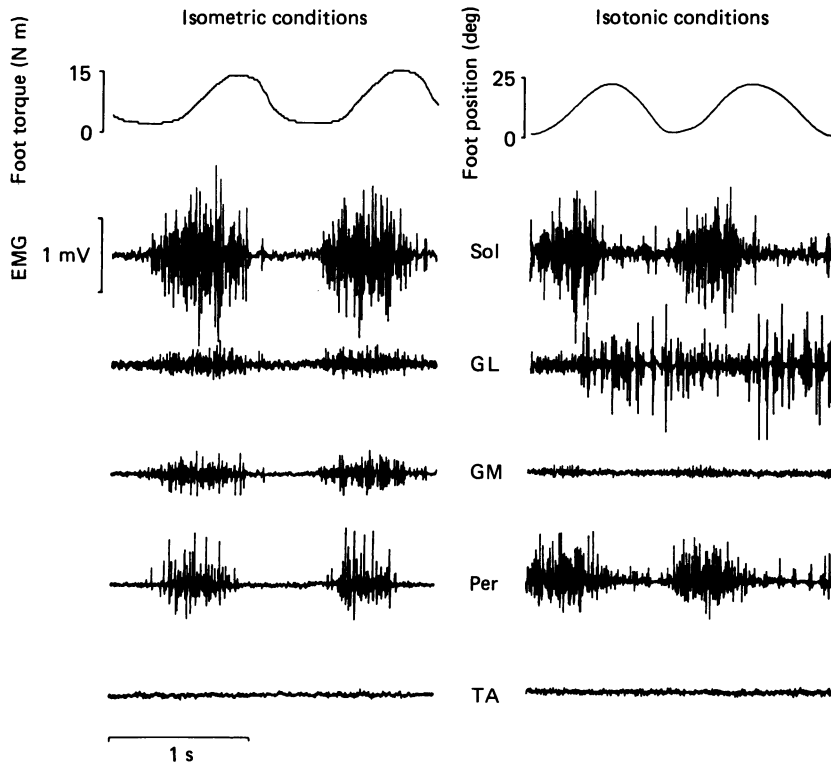

Fig. 2. Patterns of EMG activity during isometric (left panel) and isotonic (right panel) sinusoidal triceps surae contraction in one subject. On the left, EMG of triceps surae and peroneus muscles gradually increase and decrease during the phases of torque rise and decay, respectively. On the right, plantar flexion is accomplished by gradual increase in activity of soleus and peroneus muscles, both gastrocnemii being only slightly activated. In the following dorsal flexion, gastrocnemius lateralis shows a burst of activity composed of conspicuous large motor unit potentials. For abbreviations see legend to Fig. 1.

under isotonic conditions the behaviour of the muscles is similar to that observed during isotonic plantar (Fig. 1C) and dorsal flexions (Fig. 1D). In fact, during the phase of plantar flexion, EMG activity increases in parallel in all the muscles, while during the phase of dorsal flexion, bursts of large motor unit activity appear in the gastrocnemius lateralis muscle when the other muscles are silent.

Release and hold condition

When the subject was asked to initiate a dorsal flexion and to terminate it prior to reaching the point at which the pedal was blocked, by sustaining the load with an appropriate effort, the gastrocnemius laterialis muscles again increased its activity to
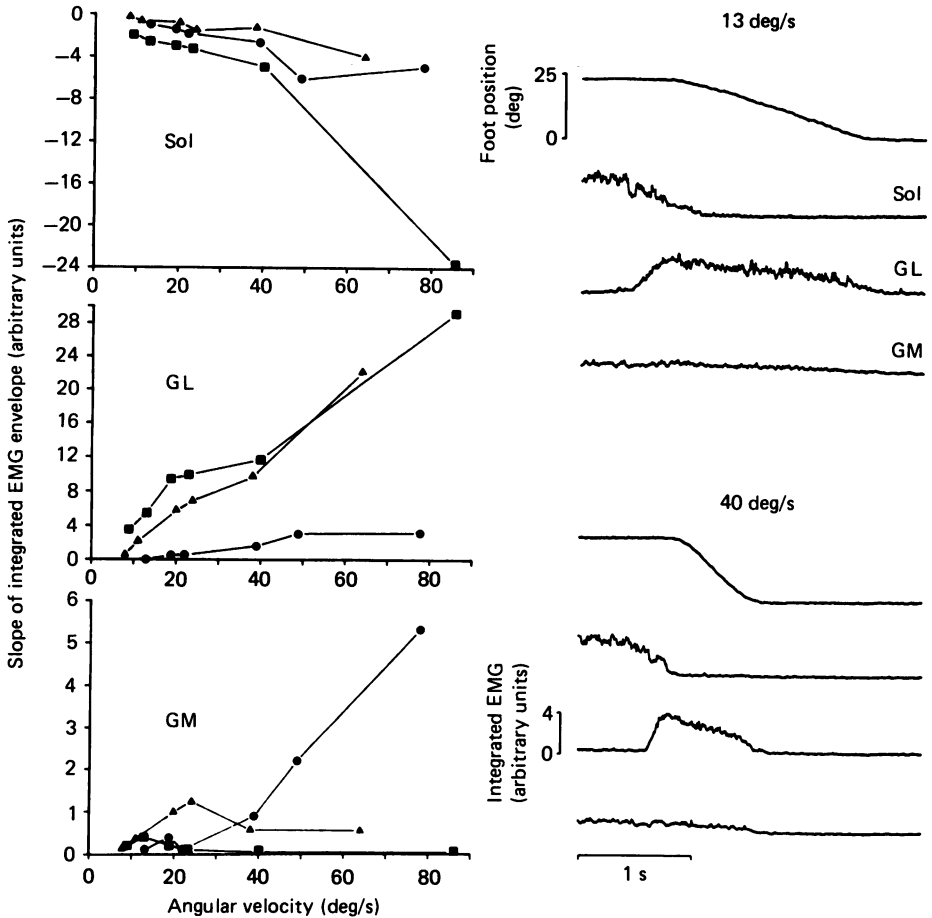
Fig. 3. Rate of soleus EMG derecruitment and gastrocnemii recruitment as a function of angular velocity of dorsal flexion. The graphs on the left show the changes in the slope of the integrated EMG envelopes of the triceps surae muscles (top, soleus (Sol); middle, gastrocnemius lateralis (GL); bottom, gastrocnemius medialis (GM)) in three different subjects (identified by the same symbols). It is shown that the higher the angular velocity, the higher the rate of soleus derecruitment and gastrocnemii recruitment. On the right, the upper and lower panels represent foot position and triceps surae muscle integrated EMGs (averages of twenty trials) from one subject (■ in the left graphs) during dorsal flexions performed at two angular velocities.

an extent similar to that occurring during complete dorsal flexion. The muscle was slowly and gradually derecruited during the following period of isometric tonic contraction. In contrast, soleus EMG activity, which almost completely disappeared during the dorsal flexion, began to increase again following completion of the dorsal rotation to reach a level needed to maintain the load at that position.

Effects induced by changing the velocity of lengthening contraction on the activation pattern of the triceps surae muscles

The right panel of Fig. 3 shows the integrated EMGs of the triceps surae muscles during dorsal foot flexions performed at two angular velocities in a subject displaying

clear-cut gastrocnemius lateralis activation. It is evident that integrated EMG of the soleus muscle starts decreasing prior to foot rotation, arriving at very low levels even at the beginning of dorsal flexion. The integrated EMG of the gastrocnemius lateralis increases prior to movement onset and reaches a peak around the beginning of it. On the left, the slopes of the line, fitted by eye to the profile of the decreasing soleus
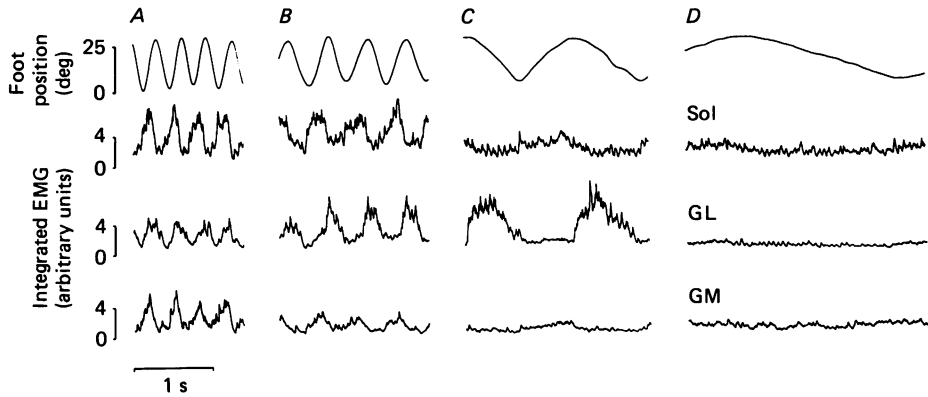

Fig. 4. Patterns of triceps surae muscle activity during sinusoidal foot movements (top traces), performed at four different velocities by one subject. Each integrated EMG trace represents one trial (in this case the time constant was 50 ms). At intermediate frequencies of oscillation (centre panels), soleus and gastrocnemius lateralis integrated EMG are out of phase, the activity of the latter occurring during the period of dorsal flexion. At the fast velocity (left), all muscles are active, and nearly in-phase, during the shortening contractions, and the dorsal flexions are simply performed by muscle relaxation, while at slow velocity (right), gastrocnemii contribution, although negligible, returns in phase. For abbreviations see the legend to Fig. 1.

integrated EMG envelope (top graph) and to the front of the increasing integrated EMG of the gastrocnemius lateralis (middle graph) and medialis (bottom graph) muscles, are plotted for three subjects against the velocity of rotation. It is evident that, within an ample range of intended velocities of foot flexion, the higher the angular velocity, the higher the rate of gastrocnemius lateralis (or medialis) motor unit recruitment. When the foot rotation in the dorsal direction increases above 100 deg/s, the gastrocnemius laterialis and medialis peak activity starts decreasing and progressively disappears, as the conditions approach those of abrupt full relaxation of the triceps, thus yielding a rapid dorsal flexion caused by the load being no longer resisted by muscle contraction.

Triceps muscles' EMG during sinusoidal isotonic contractions of various frequencies

The effect of velocity of foot rotation on the activation pattern of the triceps muscles is also observable during performance of sinusoidal rotations at various angular velocities. The foot rotations at a very high rate were performed by the subjects as a series of brisk contractions and complete relaxations, the weight of the load being sufficient to return the foot to the dorsiflexed position with the appropriate velocity. Accordingly, in this case all the muscles were active and were silenced nearly simultaneously during the phases of plantar and dorsal flexion, respectively.
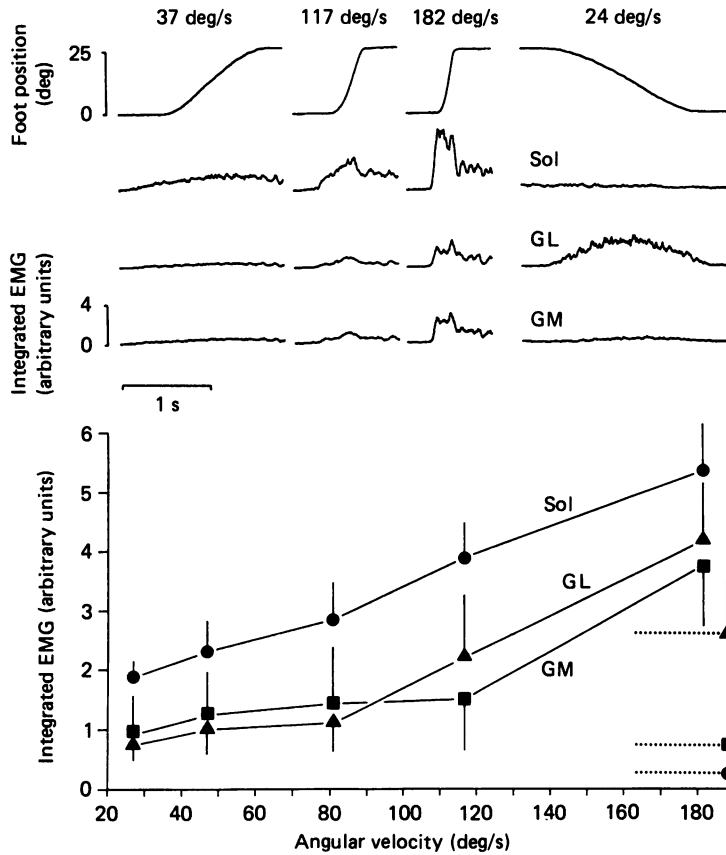
Fig. 5. Triceps surae muscle integrated EMGs during dorsal and plantar flexions. Upper panel shows foot positions and triceps surae muscle activity recorded from one subject performing three plantar flexions and one dorsal flexion at the indicated velocities (average of twenty trials). The graph represents the means of the peak amplitude (+ or − standard deviation, s.D.) of the averaged integrated EMGs (● soleus (Sol), ▲ gastrocnemius lateralis (GL), and ■ medialis (GM)) from four subjects, plotted as a function of the angular velocity of plantar flexion. The dotted lines represent the mean of the peak amplitude of the averaged integrated EMGs recorded during the dorsal flexion. It is shown that, during shortening contraction, all the integrated EMGs increase almost linearly with velocity, but the amplitude of the gastrocnemius lateralis integrated EMG exceeds that reached during lengthening contraction only in the case of the fastest, ballistic plantar flexion.

At slower frequencies of oscillations, at which voluntary control began to be exerted in order to follow the imposed rhythm, gastrocnemius lateralis activity began to fall behind soleus or gastrocnemius medialis activity, the lag increasing as a function of the decrease in frequency of the rotations. The performance of rotations at these frequencies was reportedly more difficult and required more attention. The corresponding patterns of activation are shown in Fig. 4A, B and C. When the frequency of oscillation was decreased even more, the gastrocnemius lateralis activation returned in phase with that of the other two muscles (Fig. 4D).
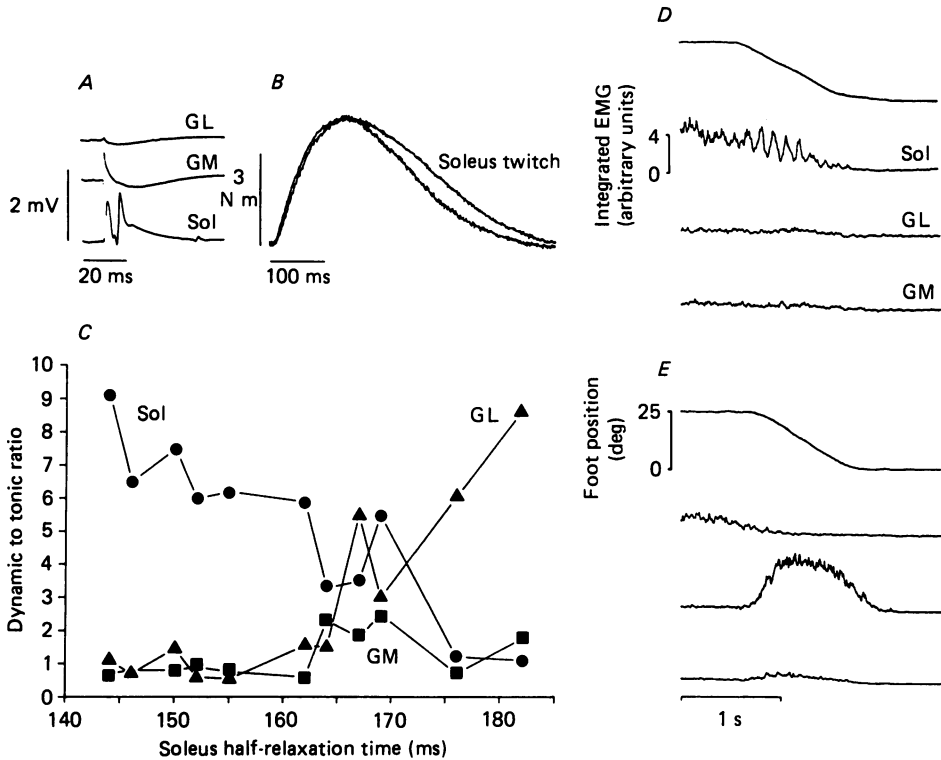
Fig. 6. Relation between patterns of triceps muscle activation during lengthening contraction and soleus twitch. *A*, EMG of triceps surae muscles (gastrocnemius medialis (GM), lateralis (GL) and soleus (Sol), from top to bottom) on stimulation of the inferior soleus nerve. M response is present in soleus only. Also indicated is the small H reflex, which occurred when the subjects were asked to voluntarily innervate the muscle (see Methods). *B*, superimposed soleus twitches of different time course, evoked at rest by the stimulation in two subjects whose integrated EMG patterns of triceps surae muscles activation are depicted in *D* and *E*. The faster twitch belongs to *D*, the slower to *E*. The graph plots the dynamic to tonic ratio (DTR) of the triceps surae muscles (● Soleus (Sol), ▲ gastrocnemius lateralis (GL) and ■ medialis (GM)) as a function of the soleus half-relaxation time of each subject (the DTR value for the soleus is obtained by dividing the corresponding values on the ordinate by 10). It is shown that the slower the soleus twitch, the larger the gastrocnemius recruitment, and vice versa, and the slower the twitch, the more is soleus derecruited, and vice versa. The equations of the lines best fitting the data are: $y = -0.02 \, x + 3.4$ (soleus), $\ln y = 0.06 \, x - 9.6$ (gastrocnemius lateralis), $y = 0.03 \, x - 3.3$ (gastrocnemius medialis); the slope of the lines and the correlation are significant ($P < 0.01$) for soleus and gastrocnemius lateralis.

Comparison of gastrocnemius recruitment between dorsal flexion and plantar flexion performed at various velocities

Since gastrocnemius lateralis recruitment was often greater during dorsal than plantar flexions at the same rotation velocities, a comparison was made between the amplitude of the triceps muscles' integrated EMG recorded during the dorsal flexion, performed at about 25 deg/s, with that observed during plantar flexions performed at various velocities. To this aim, the peak amplitudes of the integrated EMG envelopes, reached during plantar flexions of different velocities, were averaged in
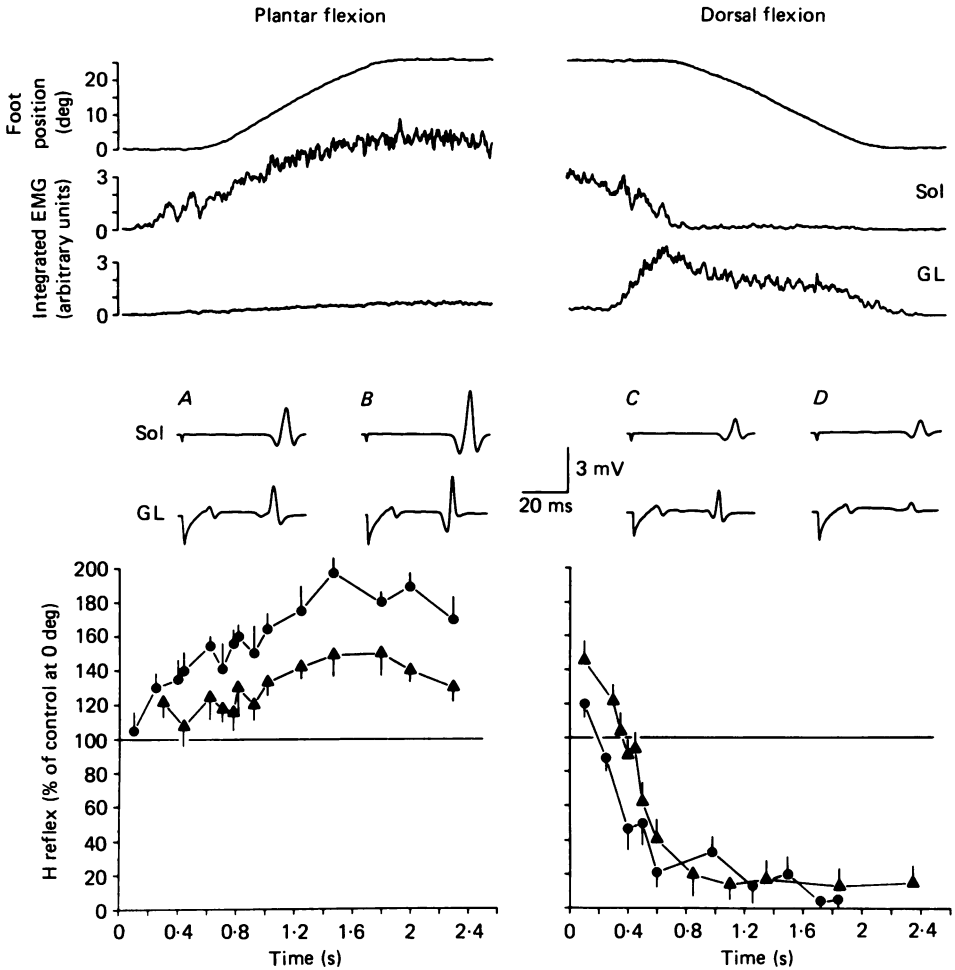
Fig. 7. H reflex of soleus and gastrocnemius lateralis muscles during shortening (left panel) and lengthening (right panel) contraction. Upper records show foot position and integrated EMGs of soleus (Sol) and gastrocnemius lateralis (GL) during both tasks in one subject (average of thirty trials). The graphs represent the time course of excitability of the H reflexes (●, soleus; ▲, gastrocnemius lateralis) expressed as a percentage of their amplitude in rest conditions (graph time base refers also to top records). Each symbol is the mean of ten measurements (+ or − s.d.). Insets are averages of ten reflexes (upper trace, soleus; lower trace, gastrocnemius lateralis) evoked at the beginning (0·5 s, *A* and *C*) and during (1·4 s, *B* and *D*) the tasks.

four subjects displaying clear-cut gastrocnemius lateralis recruitment during dorsal flexions. The bottom graph of Fig. 5 and the first three top panels show that integrated EMG peak amplitude increases in all the muscles as a function of the velocity of voluntary plantar flexion. Also shown, by dotted lines, is the level reached by the three EMGs during the dorsal flexion (top-right panel). It is evident that during ramp plantar flexions the amplitude of gastrocnemius lateralis EMG never exceeds that observed during dorsal flexion. This occurs only in case of rapid ballistic plantar contractions.

Relationship between patterns of triceps muscles' activation and soleus mechanical characteristics

During controlled dorsal flexions, some subjects used the gastrocnemius lateralis muscle for braking the load, and some the soleus. The possibility was then investigated that subjects preferentially activating soleus during dorsal flexions had a triceps muscles motor unit composition different from that occurring in those preferentially activating gastrocnemius lateralis or medialis. The former subjects might have, in fact, a relative prevalence of fast over slow motor units in the soleus muscles with respect to the latter, and therefore a faster twitch. Indirect support for this hypothesis is given by the results reported in Fig. 6. The graph plots the dynamic to tonic ratio (DTR) of the three muscles as a function of the soleus half-relaxation time in the eleven subjects investigated. In *D* and *E*, two opposite patterns of triceps muscles' activation during dorsal flexion are shown for two subjects, while in *B*, the twitches of the corresponding soleus muscles are superimposed. It appears that in the various subjects, the faster the soleus relaxation, the larger the soleus muscle recruitment, while the slower the soleus relaxation, the greater the gastrocnemius lateralis recruitment during dorsal flexion.

Reflex excitability of the triceps motoneurone pools during shortening or lengthening contractions

The excitability of the soleus and gastrocnemius lateralis motoneurone pools was tested by means of the H reflex during plantar and dorsal flexions in four subjects, in whom the muscles' reciprocal behaviour during dorsal flexions exhibited the two opposite patterns. In both cases, the excitability changes of the soleus and gastrocnemius lateralis motoneurones varied in parallel during both plantar and dorsal flexions. In particular, the H reflex amplitude increased in the soleus and gastrocnemius lateralis muscles, along with the build-up of their EMGs, during the shortening contractions leading to plantar flexion, and decreased in both muscles to well below the amplitude at rest during the dorsal flexions, irrespective of the presence of a large gastrocnemius lateralis recruitment. A typical result is shown in Fig. 7, which presents data obtained from a subject displaying rapid soleus derecruitment and large gastrocnemius lateralis recruitment during dorsal flexion.

DISCUSSION

This work has demonstrated that during triceps surae voluntary lengthening contractions, such as occur when braking a foot-dorsiflexing load, the triceps muscles undergo peculiar patterns of activation, comprising two extremes: (1) the slow soleus is rapidly relaxed, and the fast gastrocnemii (the lateralis in most subjects) take upon themselves the task of scaling the force in order to comply with intended behaviour, (2) the gastrocnemii are recruited to a lesser extent than in the above case, but bursts of high-amplitude spikes, probably generated by large, fast-twitch motor units (Olson, Carpenter & Henneman, 1968), appear in the soleus EMG recording superimposed on low-amplitude background activity. Both patterns contrast with that observed during shortening or isometric contractions, when a gradual activation

progresses in parallel in all the muscles, and also with that observed during isometric relaxations in which the time course of the derecruitment is roughly parallel in the three muscles.

This result is confirmed by the observation that controlled sinusoidal movements of plantar and dorsal flexions are performed by soleus contraction during plantar flexion and by gastrocnemius contraction (or by fast soleus motor units) during dorsal flexion. Isometric waxing and waning plantar torques, on the other hand, are sustained by gradual and parallel recruitment and derecruitment of motor units in all the triceps surae muscles. The pattern of activation of the peroneus shows gradual recruitment and derecruitment under all circumstances, in spite of its partially synergic action with that of the triceps surae, as during foot plantar–dorsal rotation it contracts or relaxes in a nearly isometric way, since no foot extrarotation occurs during the tasks.

The different behaviour observed under isotonic and isometric conditions was not unexpected because the analogies of the two tasks are more apparent than real. Under isometric conditions, force decreases from a given value to zero, and the rate of force decrease may match closely the time course of the changes in foot position during dorsal flexion, i.e. the angular velocity of foot rotation, even in the case of very rapid dorsal flexions. Under isotonic conditions, however, the overall force generated by the muscle remains constant throughout dorsal flexion. Besides, within the limited range of angular positions reached during the task, the force actively generated by the contractile material changes little as well, solely as a function of the shift in the force–length diagram. Under isotonic conditions in which gravity acts upon the load, the subjects use a strategy that can be envisaged as consisting of short-lasting relaxations (allowing the load to drop) followed by contractions (holding the load in the new position). Such a process would contain the required features of smoothness and skill, even during the most rapid lengthening contractions, the more the force 'quanta' decrease in duration, and to this aim the fast muscles or motor units appear the most appropriate. When, after a partial dorsal flexion, the load must be held in position for an extended period of time, soleus recruitment gradually recommences while the gastrocnemius lateralis becomes silent. Alternatively, units with minimal force output could contribute to the task and help in performing a smoothly fused lengthening contraction. But the smaller motor units are also the slowest ones, and therefore have the lowest velocity of relaxation; they are used, in fact, by all subjects during the slowest lengthening contractions but not during the faster ones, at which time they would represent a mechanical disadvantage.

The velocity of active muscle lengthening appears critical for the shift in activation from soleus to gastrocnemius lateralis to appear. The gastrocnemii are active in the higher range of angular velocities of foot rotation in the dorsal direction. Their activity disappears at all but the highest velocities of dorsal flexions, approaching full relaxation and leading to a quick drop of the supported weight, or disappears under the condition of dorsal flexions performed at very slow angular velocity. Within that range, the rate of soleus motor unit derecruitment and of gastrocnemius motor unit recruitment is increased as a function of the intended velocity of dorsal flexion, indicating that the higher the velocity of the lengthening

contraction, the more important it becomes to rely solely upon the fast muscles to perform the task. Actually, this shift in activation of the two muscles begins just in advance of foot rotation and could therefore be considered a preparatory and pre-programmed process. Once initiated, the dorsal flexion is continued and brought to an end by gradual derecruitment of the fast-twitch motor units of the gastrocnemii. That the latter are actually fast, probably belonging to the fastest of the pool, is proved by the evidence that during shortening contractions, recruitment of gastrocnemius lateralis, which gave integrated EMG envelopes of an amplitude such as that observed during dorsal flexions, was obtained only by plantar flexions performed in ballistic conditions.

In about half of the subjects, the gastrocnemius lateralis or medialis muscles did not undergo the striking recruitment during dorsal flexion discussed above. Conversely, in these subjects the soleus continued to be active during the lengthening contraction, but its EMG pattern changed from one of full interference to one in which few large units fired, sometimes in a rather synchronized way. The soleus in man is not as homogeneous as it is in the cat, and its composition may vary from subject to subject (Johnson, Polgar, Weightman & Appleton, 1973; see Saltin & Gollnick, 1983). We suggest, therefore, that large motor units in the soleus were active in that case. This hypothesis is strongly supported by the finding that the soleus muscles of the subjects behaving in this manner had the shortest half-relaxation times. This observation provides an interesting counterpoint to that reported by Smith & Spector (1981), showing that during paw shaking in cats, the gastrocnemius lateralis bursts appear isolated when the soleus contraction time is slow, but are accompanied by soleus activation in cats having a rapid soleus contraction time. It may be noted, incidentally, that in our case the preferential activation of gastrocnemius lateralis was more tightly correlated with soleus half-relaxation time than with the time to peak force.

Given the hypothesis that slow-twitch motor units need not be active during a lengthening contraction, it comes as no surprise that soleus reflex excitability is drastically reduced in that task, the higher the velocity of relaxation, as already demonstrated (Romanò & Schieppati, 1987). It could, however, be questioned whether the gastrocnemii motoneurones are also subjected to the same decrease in reflex excitability. If this is so, how can gastrocnemii motoneurones fire during a lengthening contraction, given that a decrease in reflex excitability would favour motoneurone derecruitment (Schieppati, Nardone & Musazzi, 1986)? On the other hand, how could gastrocnemii motoneurones escape inhibition if it is reasonable to assume that the decrease in reflex excitability of the synergist soleus muscle is brought about by a descending command acting through enhancement of the presynaptic inhibition on the Ia terminals (see Schieppati, 1987)? Actually, the changes in the gastrocnemius lateralis H reflex parallel those in the soleus, even in the subjects in which the former is recruited and the latter is derecruited. The simplest explanation is that the H reflex tests the excitability of the slow motor units in the gastrocnemii, as has been demonstrated for the soleus (Buchtal & Schmalbruch, 1970), and these units are, in turn, subjected to the largest presynaptic inhibition (Zengel, Reid, Sypert & Munson, 1983). It is therefore conceivable that a descending, excitatory command impinges upon the triceps motoneurone pools during dorsal

flexion, together with a command to decrease their reflex excitability, acting through the presynaptic inhibitory mechanism. But as a result of the larger presynaptic effect on the I a input to the slow motoneurones, the fast motoneurones in the gastrocnemius, or even the fast motoneurones in the soleus, would be spared this decrease in autogenetic excitation, and would, therefore, be free to discharge. Such a mechanism could contribute to the capability of the motor cortex to facilitate the gastrocnemius and inhibit the soleus motor pools, as described some time ago by Preston & Whitlock (1963).

Another reason for the persistence or increase in discharge of the fast gastrocnemius motor units during dorsal flexion, i.e. during a manoeuvre that induces a marked depression in the reflex excitability of the soleus, might be the different susceptibility of the two muscles to articular input, or to input from the skin covering the heel, since (1) in the cat, large gastrocnemius motor units may be activated and small soleus motor units silenced in response to a sural input (Kanda, *et al.* 1977); (2) in man, soleus H reflex is strikingly inhibited during a passive dorsal flexion (Romanò & Schieppati, 1987). The fast-motor-unit activation could, in turn, enhance the slow-motor-unit silence through recurrent inhibition (Ryall, Piercey, Polosa & Goldfarb, 1972; Friedman, Sypert, Munson & Fleshman, 1981; Broman, De Luca & Mambrito, 1985). It is known, in fact, that the large motoneurones, connected with fast muscle fibres, give off a larger number of collaterals to the Renshaw cells than the small ones (Cullheim & Kellerth, 1978) and that small motoneurones have larger recurrent IPSPs (Eccles, Eccles, Iggo & Ito, 1961).

These considerations apparently challenge a conclusion arrived at in preceding papers from this laboratory, that enhancement of presynaptic inhibition is important in keeping motor units from being reflexly activated by the I a afferent discharge during muscle relaxation (Schieppati, Poloni & Nardone, 1985; Schieppati *et al.* 1986) and lengthening contraction (Romanò & Schieppati, 1987; see Schieppati, 1987). The present results seem to falsify the above hypothesis, showing that new motor units are recruited during dorsal flexion. However, if the latter are fast-twitch motor units, one would not expect that they would receive a I a input during muscle stretch (Burke, 1968; Bawa, Binder, Ruenzel & Henneman, 1984) large enough to induce their reflex activation (Calancie & Bawa, 1985), which would be a perturbing factor during accurately controlled lengthening contractions (see Schieppati, 1987). On the other hand, the lack of reflex activation (or facilitation, see H reflex results, Fig. 7) of the soleus motoneurones, connected with lengthening of the active gastrocnemius, which should induce a large afferent spindle discharge (Burke, Hagbarth & Löfstedt, 1978), is also in agreement with the reported virtual absence of heteronymous excitatory effects from gastrocnemius medialis to the soleus (Pierrot-Deseilligny, Morin, Bergego & Tankov, 1981). Another hypothesis held was that derecruitment was necessary in order to decrease the number of motor units active during a lengthening contraction, since each unit exerts a larger force while being stretched than while shortening (Katz, 1939). The present results show instead an increase of integrated EMG during lengthening contractions. Thus, to what aim are new motor units recruited in the triceps muscle during dorsal flexion? (1) The absolute number of active motor units need not be higher than that during a shortening contraction, as recruitment of new units (as, for example, in the

gastrocnemius) is accompanied by derecruitments of others (in the soleus). (2) The increase in the gastrocnemius lateralis integrated EMG (or in soleus in some subjects) must be considered cautiously, since the integrated EMG amplitude is not only proportional to the number of active motor units but also to their position in the muscle and to the current generated by each, which is larger in the case of fast-twitch motor units (Olsen *et al.* 1986). (3) It is likely that the relative force increments of the fast-twitch muscles during lengthening contraction are smaller than those of the slow-twitch muscles under the same conditions, if one can extrapolate to the negative part of the force–velocity graph the data obtained in humans by Thorstensson (1976) during shortening contractions of muscles of different composition (see also Spector, Gardiner, Zernicke, Roy & Edgerton, 1980, in the cat).

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